UNIVERSITY OF PENNSYLVANIA

EXCHANGE OF ELECTROLYTES BETWEEN ROOTS AND ACID SOLUTIONS

RUTH BEALL

A DISSERTATION

IN BOTANY

PRESENTED TO THE FACULTY OF THE GRADUATE SCHOOL IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

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EXCHANGE OF ELECTROLYTES BETWEEN ROOTS AND ACID SOLUTIONS[1]

RUTH BEALL

(WITH FIVE FIGURES)

Introduction

This paper presents, in abbreviated form, some results of a study of changes in electrical conductance and in hydrogen-ion concentration of dilute acid solutions exposed to the action of seedling roots of *Lupinus albus* L. Effects of these solutions on the plants are also described.

Materials and methods

Three inorganic acids (HCl, H_2SO_4, and HNO_3) and three organic acids (formic, acetic, and propionic) were tested separately, each at three concentrations, 0.00002 N, 0.00008 N, and 0.00016 N. Expressed as molar fractions these concentration values are M/25,000, M/12,500, and M/6250 for HCl, HNO_3, and the organic acids; and they are M/50,000, M/25,000, and M/12,500 for H_2SO_4. The water used was redistilled from Pyrex glass and had a conductance of approximately 2 millionths reciprocal ohm. For control cultures DOAK'S (**11**) modification of HARTWELL and PEMBER'S nutrient solution was used, as well as H_2O.

Seeds of white lupine were germinated in finely chopped sphagnum and the resulting seedlings were introduced into the test solutions when primary roots and hypocotyls were about 6 cm. and 3 cm. long, the cotyledons being still within the seed coats. After rinsing, four seedlings were introduced into each culture jar. The jars used were 500-ml. Pyrex beakers, each containing 500 ml. of liquid. The seedlings were supported by means of cotton in holes in the jar lids, which were perforated Petri-dish covers of Pyrex glass (**2**). The roots were wholly submerged and the hypocotyls were entirely above the liquid surface. Thus nearly the same area of root surface was exposed to the solution in every case.

These experiments were carried out in a dark-room at the Botanical Laboratory of the University of Pennsylvania. For each set of solutions there were two series of experiments, the temperature for one series being about 22° C. for the mineral acids, and about 23° C. for the organic acids; that for the other series being about 28° C. Temperature fluctuated somewhat in each case, within plus or minus 2°.

[1] This experimentation was carried out with the financial aid of a Lydia T. Morris Fellowship of the Morris Arboretum of the University of Pennsylvania.

Changes in ionic concentration of the solutions surrounding the roots were followed by means of daily measurements of electrical resistance, from which were derived the corresponding specific conductance values, computed for a temperature of 18° C. Daily measurements of hydrogen-ion concentration were made by means of the quinhydrone-titration method, with McIlvaine's buffers (**4**). Since the temperature coefficient of hydrogen-ion concentration is so small as to be negligible in such a study as this (**7**), the pH values were not corrected for temperature. Daily observations concerning the appearance of the plants were also made, particularly with regard to development and visible injury.

In the following subsections, changes in the media will be presented first, distilled water and the several acid solutions being considered in order, and then attenion will be turned to records of growth and of injury to the plants.

Experimentation

Changes in the media

Distilled water.—Figure 1 presents graphically average daily con-

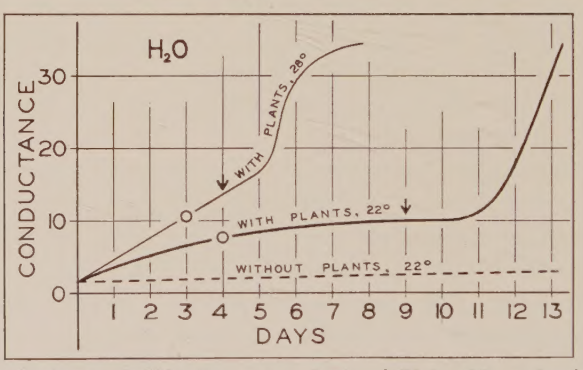

Fig. 1. Conductance (millionths recip. ohm) of H_2O with and without seedlings. Circles mark end of rapid initial increase in pH; arrows mark onset of visible root injury.

ductance values for H_2O with and without seedlings at 22° C., and for H_2O with seedlings at 28° C. Since no considerable conductance increase occurred without plants, it may be inferred that the increases shown by water with plants were due to outward movement of material from the roots. There was continuous exosmosis of electrolytes, in excess of any absorption that may have occurred. Net exosmosis, which was at first relatively slow, became markedly accelerated about the fifth day at the higher temperature and about the eleventh day at the lower temperature. It was at all times more rapid at the higher temperature than at the lower. At the lower temperature the pH value of H_2O with seedlings increased from 5.4 to 5.7 in

the first day, and then to 6.1 in the following three days, after which it remained practically unchanged. At the higher temperature the changes were very similar, but more rapid, from 5.0 to 5.5 in one day, and to 6.1 in three days. This may indicate either that there was some absorption of hydrogen ion, the effect of which on conductance was overbalanced by relatively greater exosmosis of electrolytes, or that exosmosis acted to reduce the hydrogen-ion concentration of the surrounding liquid.

MINERAL ACID SOLUTIONS.—The manner in which conductance of the mineral acid solutions in contact with seedling roots first decreased and subsequently increased is shown by the graphs of figures 2 to 4. Each graph

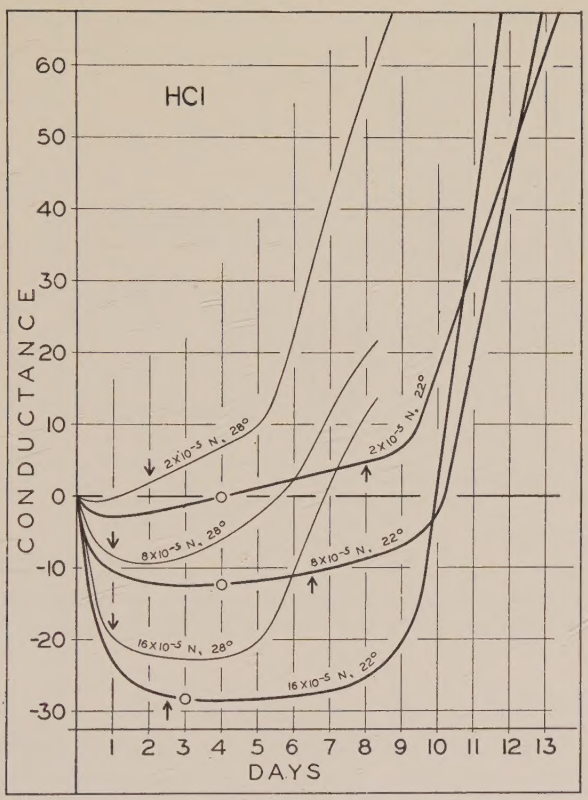

FIG. 2. Conductance change (millionths recip. ohm) in HCl solutions with seedlings. Circles mark end of rapid initial increase in pH; arrows mark onset of visible root injury.

starts at zero on the scale of ordinates (which, in each case, represents the initial conductance of the solution in question) and conductance decreases are plotted as negative while increases are plotted as positive. The three average initial conductances, expressed as reciprocal ohms $\times 10^{-6}$, for each of the three concentrations of each acid were as follows: HCl, 8.9, 26.8, 52.8; H_2SO_4, 8.8, 26.9, 56.2; HNO_3, 8.5, 31.3, 64.5.

Some special measurements made at the end of the first hour showed, in many instances, a slight initial increase in conductance, relatively greater as the original concentration of the solution was higher, which suggests that there may have been an immediate exosmosis of electrolytes from the roots. This detail is not shown on the graphs; it was not seriously studied and warrants no more than mention here.

Each of the graphs shows an initial decrease in conductance, which was very slight and of very short duration for the solutions of lowest concentration, but progressively more pronounced and of longer duration as concentration was higher. Considering the two graphs for each concentration together, it may be said that the period of conductance decrease was shortest

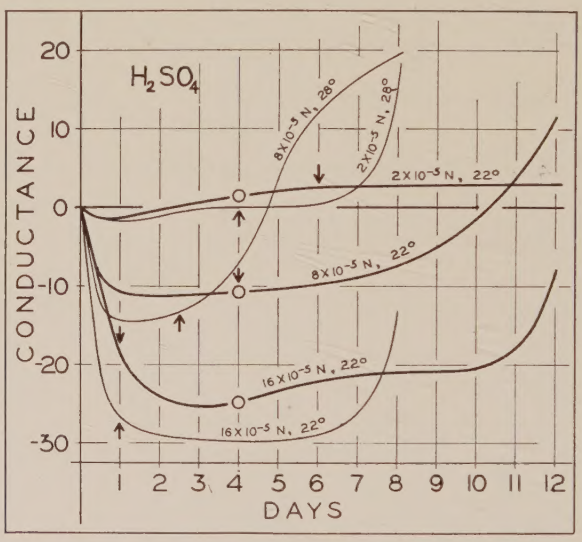

FIG. 3. Conductance change (millionths recip. ohm) in H_2SO_4 solutions with seedlings. Circles mark end of rapid initial increase in pH; arrows mark onset of visible root injury.

(about 1 day or less) for the lowest concentration, longer (about 2 to 3 days) for the intermediate concentration, and longest (about 3 to 4 days) for the highest concentration. Similarly, the average amounts of conductance decrease were approximately as follows, the unit being 1×10^{-6} reciprocal ohm: for the lowest concentration, 2 units (all three acids); for the intermediate concentration, 11 units (HCl), 13 units (H_2SO_4), and 17 units (HNO_3); for the highest concentration, 26 units (HCl), 28 units (H_2SO_4), and 41 units (HNO_3). It is notable that HNO_3 showed greater conductance decrease at the two higher concentrations than was shown by either of the other mineral acids at these concentrations.

As to the temperature relations of the amount of conductance decrease, the available data permit no satisfactory generalization for all three mineral acids. From the graphs of figure 2 it is clear that the amount of conductance decrease for solutions of HCl was regularly somewhat greater at the lower than at the higher temperature. For the lowest and highest concentrations of HNO_3 (fig. 4) the same temperature relation apparently holds, but for the intermediate concentration of HNO_3 and for all tested concen-

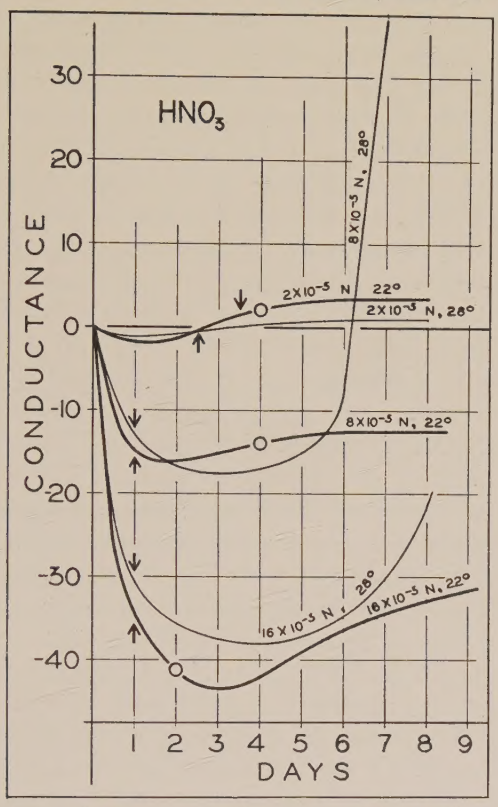

FIG. 4. Conductance change (millionths recip. ohm) in HNO_3 solutions with seedlings. Circles mark end of rapid initial increase in pH; arrows mark onset of visible root injury.

trations of H_2SO_4 (fig. 3) conductance decrease was more or less markedly greater at the higher than at the lower temperature.

When conductance decrease was relatively large in amount its rate is seen to have been rapid at first and then progressively more gradual. For the intermediate and highest concentrations the initial period of decrease was followed by a more or less prolonged period during which conductance was nearly maintained. This period was longer for the lower temperature

than for the higher one. After conductance began to increase, its rate of change sometimes remained low to the end of the experimental period, but in many cases (notably all the graphs of figure 2) its rate was soon rapidly accelerated, so that the final portions of the graphs ascend very steeply.

As to changes in hydrogen-ion concentration, the pH values of all tested solutions—and that of H_2O also—increased from the beginning of the experimental period onward. This increase was most rapid during the first day and became progressively slower till a value of about 6.0 was reached, when hydrogen-ion equilibrium with the roots was apparently established. Eventually the solutions became slightly more basic. The initial pH values of the solutions, corresponding to the initial conductances given above, were as follows: HCl, 4.6, 3.9, 3.6; H_2SO_4, 4.5, 3.9, 3.6; and HNO_3, 4.5, 3.8, 3.5. After one day the following values were reached: HCl, 4.8, 4.6, 5.3; H_2SO_4, 5.1, 4.6, 5.5; and HNO_3, 4.9, 5.1, 5.6. The time required, at the lower temperature, for each medium to attain a pH value of about 6.0 is shown by the position of the circle on the corresponding graph of figures 1 to 4. That time was in general somewhat shorter for the solutions of highest concentration than for the other solutions and for H_2O. The two lower concentrations of the three acids were essentially alike, reaching this value in four days; for the highest concentration the change was somewhat more rapid in HNO_3 (2 days) than in HCl (3 days) or H_2SO_4 (4 days).

Organic acid solutions.—Conductance changes shown by the three organic acids in contact with seedlings are set forth by the graphs of figure 5, which are plotted like those of figures 2 to 4. For each of the three concentrations of each acid, the initial conductance (each plotted as zero on the ordinate scale) was as follows: HCOOH, 6.2, 16.2, 29.3; CH_3COOH, 5.5, 10.6, 16.3; C_2H_5COOH, 4.2, 9.6, 14.1. For each solution the two temperatures tested showed no essential differences in conductance change; the graphs of figure 5 represent the average values for the two temperatures. As in the case of the mineral acids, conductance measurements made within the first day of the experimental period indicated in some instances a very slight immediate increase in conductance, of very short duration, which is not shown on the graphs.

These organic acid solutions showed an initial decrease in conductance, similar to that shown by the mineral acid solutions, but less pronounced. For the lowest concentration of each acid this decrease was of one day's duration or less. It was scarcely noticeable in the case of the most dilute solution of propionic acid, only very slight in the weakest acetic acid solution, and somewhat more pronounced in the lowest concentration of formic acid. In all these cases conductance subsequently increased gradually for about three days, after which it remained approximately unchanged. For

solutions of higher concentration the initial conductance decrease lasted somewhat longer, from one to three days, after which there was, in most cases, some increase, but this was never sufficient to raise the conductance of the solution above its original value. In general, conductance remained unchanged after five days. As was shown for the inorganic acid solutions, initial decrease was greater in amount as solution concentration was greater, the amounts of decrease (in conductance units) being as follows: HCOOH, 2, 11, 20; CH_3COOH, 1, 4, 8; C_2H_5COOH, 0.1, 3, 6.

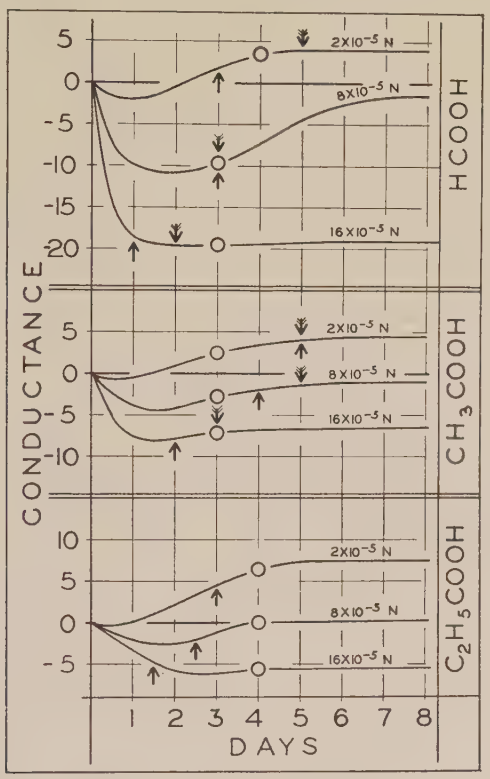

FIG. 5. Conductance change (millionths recip. ohm) in organic acid solutions. Circles mark end of rapid initial increase in pH; winged arrows mark onset of visible root injury at 23° C., naked arrows at 28° C.

Only the graphs for the lowest concentration of acetic acid and of propionic acid and the ones for the lowest and intermediate concentrations of formic acid show any considerable conductance increase within the 8-day period, but of course the conductance of the other organic acid solutions might have increased eventually had the period been longer. To make possible satisfactory comparisons among all six acids, with reference to con-

ductance increase, it would apparently have been necessary to employ experimental periods longer than 8 days.

Turning to the changes in hydrogen-ion concentration of the organic acid solutions, these were very nearly like the corresponding changes that occurred in the mineral acid solutions, except that the original solutions were generally less acid and the amount of change was correspondingly less. The initial pH values of the three concentrations of each of the three organic acids were as follows: HCOOH, 4.5, 3.9, 3.6; CH_3COOH, 4.8, 4.5, 4.1; and C_2H_5COOH, 4.9, 4.5, 4.2. In general there was rapid decrease in acidity during the first day, the following pH values being reached: HCOOH, 5.6, 5.7, 5.8; CH_3COOH, 5.5, 5.3, 5.3; and C_2H_5COOH, 5.3, 4.5, 4.3. Subsequently the decrease in acidity continued, but was more gradual, the solutions attaining a value of about 6.0 by the end of 3 days (intermediate and highest concentration of HCOOH and all three concentrations of CH_3COOH) or at the end of 4 days (lowest concentration of HCOOH and all concentrations of C_2H_5COOH), after which pH was approximately maintained. These times are indicated by the positions of the circles on the graphs of figure 5.

Physiological effects

Controls.—On the roots of the control plants, in nutrient solution, lateral branches always appeared within the first day of the experiment and these subsequently increased in number and enlarged as the primary root continued to elongate. On the second day, when the hypocotyl was well extended, the cotyledons diverged, and later the plumule opened and elongation of the epicotyl began. No chemical injury was apparent and these plants appeared to be quite healthy throughout the entire experimental period of 14 days, excepting that, being in darkness or very weak light, they were markedly etiolated.

Plants with roots in water.—Seedlings with roots in H_2O developed more slowly than those with roots in nutrient solution. Development of lateral roots was similar to that in nutrient solution except that these did not appear until after 2 days and they did not elongate so much. After 2 days also the cotyledons began to diverge and gradually development of the epicotyl proceeded. Injury at the tips of the roots was evident after about 9 days at the lower temperature and after about 4 days at the higher temperature, as is indicated by the arrows of figure 1. Injury to hypocotyls followed in many cases.

Plants with roots in mineral acid solutions.—In solutions of mineral acids development was still more retarded than in water and injury was apparent earlier. Injury was first noticeable as a slight constriction in the primary root, 1 to 2 mm. from the tip. The tip region soon became

flaccid and translucent, then very soft and brown. These changes gradually spread upward until, in the most severe cases, only the upper centimeter or less of the root was apparently free from necrosis. Injury to the hypocotyl usually followed soon after the onset of root injury. It was first evident as a translucent region 1 to 2 cm. long, about the middle of the hypocotyl, and necrosis spread both upward and downward. Subsequently the injured region of the hypocotyl turned brown and collapsed, sometimes with exudation, whereupon the cotyledons and plumules drooped. The plumule developed only slightly or not at all.

Development in the mineral acid solutions was roughly in inverse relation to the original concentration of the solution. Neither primary root nor hypocotyl elongated to any considerable extent in the solutions of highest concentration and both showed less elongation in the solutions of intermediate concentration than in the most dilute solutions. Lateral roots appeared after 2 days in all cases; in solutions of lowest concentration they developed throughout practically the entire length of the primary root, in solutions of intermediate concentration they were confined to the upper two-thirds of the main root, and in solutions of highest concentration they were confined to the upper one-third or less. When the region of their development was restricted they were unusually crowded. At the end of the experimental period they were longer in all mineral acid concentrations than in water, and their length was greater as the region supporting them was shorter. At either temperature, injury to the roots became evident earlier and progressed more rapidly as solution concentration was higher, and for any tested concentration it appeared earlier and progressed more rapidly at the higher than at the lower temperature. At the end of the experimental period injury in the least concentrated solutions was confined to the terminal region of the primary root, in solutions of intermediate concentration it occupied from one-third to one-half of the length of the main root, and in solutions of highest concentration the primary root was visibly injured throughout practically its entire length. Injury to the hypocotyls also appeared earlier and progressed more rapidly as the solution was more concentrated and as the temperature was higher. If the times required for the onset of root injury in these solutions (as shown by the positions of the arrows in figures 2 to 4) are considered roughly as reciprocally proportional to the toxicity of the solutions, then it appears that, for the two lower concentrations at the lower temperature, the decreasing order of toxicity for these three mineral acids was HNO_3, H_2SO_4, HCl. For the highest concentration at this temperature HNO_3 and H_2SO_4 were about alike and produced injury sooner than HCl. For the lowest and for the intermediate concentration at the higher temperature HNO_3 and HCl were about alike and produced injury more promptly than H_2SO_4. Finally, all three acids were approximately alike, on the basis of this time criterion, for the

highest concentration at the higher temperature since all had produced injury within the period before the first examination, but in these cases injury was noticeably more severe in HNO_3 solutions than in the other acids. It thus appears that both temperature and concentration took part —along with the chemical characteristics of the acids—in determining the promptness of the onset of injury.

Plants in organic acid solutions.—Development was more rapid and more extensive in the solutions of organic acids than in the corresponding solutions of mineral acids. With formic and acetic acids development was somewhat greater in the lowest concentrations than in the others; with propionic, however, development in the solution of intermediate concentration equalled or exceeded that in the most dilute solution, and development in the most concentrated solution was less rapid than in either of the other solutions. By the second day lateral roots had emerged in all cases. They appeared earlier, however (after only 1 day), in the most concentrated solutions of formic acid and acetic acid at the higher temperature, and in all solutions of propionic acid at this temperature. Like the mineral acids tested, the organic acids permitted the development of laterals throughout most of the length of the primary root in solutions of lowest concentration. As the solution was more concentrated laterals were increasingly restricted to the older region of the primary root, but the region bearing laterals was not so limited as under the corresponding influence of the mineral acids. As with the inorganic acid solutions, but to a lesser extent, lateral roots were finally more closely crowded and longer the more restricted was the region from which they arose.

Injury by the organic acids was similar, in inception and nature, to that produced by the mineral acids, but for any tested concentration and temperature it generally appeared somewhat later with the most rapidly injurious organic acid than with the least rapidly injurious mineral acid, as is shown by comparing the positions of the arrows on the graphs of figures 2 to 5. (It should be noted that in figure 5 winged arrows refer to the lower temperature while naked arrows refer to the higher temperature.) Acetic acid generally appears to have been less promptly injurious than either of the other organic acids, which were apparently about alike in this respect. In general, injury by any solution was less prompt at the lower than at the higher temperature and it appeared sooner as the concentration was higher.

The six acids and H_2O compared as to toxicity

Although the available data are inadequate for a satisfactory comparative study of the degrees of toxicity of all six acids, it may be of interest to summarize the lengths of time required for the onset of visible root injury, as follows:

1. At 22° or 23° C. the descending order of indicated toxicity for each concentration is:
   a. For lowest concentration: HNO_3 (3.5 days), HCOOH and CH_3COOH (5 days), H_2SO_4 (6 days), HCl (8 days).
   b. For intermediate concentration: HNO_3 (1 day), HCOOH (3 days), H_2SO_4 (4 days), CH_3COOH (5 days), HCl (6.5 days).
   c. For highest concentration: HNO_3 and H_2SO_4 (1 day), HCOOH (2 days), HCl (2.5 days), CH_3COOH (3 days).
2. At 28° C. the descending order of indicated toxicity for each concentration is:
   d. For lowest concentration: HCl (2 days), HNO_3 (2.5 days), HCOOH and C_2H_5COOH (3 days), H_2SO_4 (4 days), CH_3COOH (5 days).
   e. For intermediate concentration: HNO_3 and HCl (1 day), H_2SO_4 and C_2H_5COOH (2.5 days), HCOOH (3 days), CH_3COOH (4 days).
   f. For highest concentration: HNO_3, H_2SO_4, HCl and HCOOH (1 day), C_2H_5COOH (1.5 days), CH_3COOH (2 days).

For each combination of temperature and concentration the reciprocal of the injury-time for each acid may perhaps be taken as an index of its relative toxicity. If for each combination all six reciprocals are expressed in terms of the reciprocal for HNO_3 and if the resulting relative toxicity values for each acid are averaged, the final outcome is a single series of tentative toxicity indices that may represent all the tested combinations of temperature and concentration; that new series is as follows: HNO_3, 1.00; HCl, 0.71; H_2SO_4, 0.66; C_2H_5COOH, 0.63; HCOOH, 0.61; CH_3COOH, 0.41. The corresponding value for H_2O is 0.22. According to these averages, it appears on the whole: (a) that HNO_3 was the most toxic, while (b) CH_3COOH was least toxic of the six acids considered, (c) the former being about 2.5 times as toxic as the latter; (d) that HCl and H_2SO_4 were nearly alike in toxicity (about 69 per cent. as toxic as HNO_3); (e) that C_2H_5COOH and HCOOH were nearly alike in toxicity (about 62 per cent. as toxic as HNO_3), (f) only slightly less toxic than HCl and H_2SO_4, and (g) about 50 per cent. more toxic than CH_3COOH; and, finally, (h) that H_2O appeared to be about half as toxic as CH_3COOH and about one-fifth as toxic as HNO_3. While these statements seem to agree in general with some conclusions that are suggested by superficial scrutiny of the graphs and their appended arrows, it must be remembered that they are intended only to represent a sort of summary of the toxicity phase of the present study, for it is almost certain that the degrees of toxicity of these acids in any test depend on temperature and concentration as well as on chemical nature.

Conclusion

The initial reduction in conductance of these acid solutions was evidently due to absorption of ions by the roots. This absorption was probably accompanied by some exosmosis in all cases, as was shown for H_2O.

While it is conceivable that the conductance of a solution might be diminished by exosmosis alone, if the materials extruded from the roots were of such nature as to remove from solution the ions present, consideration of the nature of the solutions examined in this study and of the kinds of material that might possibly escape from plant roots leads to the conclusion that the observed conductance decrease must have been due to direct removal of ions by the plants. This was no doubt accomplished principally by absorption of material into the cells, but adsorption of ions on to root surfaces may have occurred also. Since solutions of all the acids tested were reduced in conductance, and hence in ion concentration, it seems safe to conclude that ions were absorbed from both inorganic and organic acid solutions.

The amount of net absorption from the several solutions seems to have varied directly with ion supply. For any acid, the higher the ionic concentration of the original solution, the greater and more rapid was the removal of electrolytes. And among the six acids tested, the greater the degree of ionization, in general, the more rapid was net absorption. A general index of absorption from these acid solutions under all the conditions represented by these experiments may be derived by expressing the average amount of net absorption from each concentration of each acid in terms of the average net absorption from the corresponding concentration of HNO_3, and averaging the three values for each acid. This index is as follows: HNO_3, 1.0; H_2SO_4, 0.83; HCl, 0.77; HCOOH, 0.73; CH_3COOH, 0.30; and C_2H_5COOH, 0.12. That is, considering the average of the results of the several experiments, there was greatest absorption from HNO_3 solutions, and least from those of C_2H_5COOH. Net absorption from the organic acid solutions was generally less than from the corresponding concentrations of mineral acids, but HCOOH was only slightly below HCl and H_2SO_4 in this respect. This is in general agreement with the order of dissociation of these acids.

Absorption was, however, apparently influenced by other factors to some extent. Examining the results for the two temperatures separately it may be seen that, for the several mineral acids at the lower temperature, net absorption from HNO_3 solutions was greatest and that from H_2SO_4 solutions was least, net absorption from HCl being intermediate. This order of penetration ($HNO_3 > HCl > H_2SO_4$) is in agreement with Davidson and Wherry's (**9**) results with wheat seedlings. On the other hand, in the present study the order of penetration at the higher temperature is: $HNO_3 > H_2SO_4 > HCl$; this is the order reported by Hind (**15**) from her experiments with potato tuber. Net absorption was apparently increased by rise in temperature in the case of all solutions of H_2SO_4 and the intermediate concentration of HNO_3, but in the case of the other solutions (namely, all concentrations of HCl and the lowest and highest con-

centrations of HNO_3) net absorption was apparently decreased. DELF (**10**) and SKEEN (**20**) found the permeability of plant tissues to increase with rise in temperature, and STILES and JØRGENSEN (**24**) report greatly augmented absorption of hydrogen ion under similar conditions. ECKERSON (**13**), on the other hand, reports that the effect of rise in temperature on permeability of root cells varied according to the species considered. Studies on this subject reported in the literature have been carried out with a variety of materials and by means of a variety of experimental procedures. It is safe to presume that rates of penetration of materials into plant roots, and rates of absorption, depend on the kind and condition of the roots as well as on temperature and the nature of the solutions from which the absorbed substances are derived.

The pronounced decrease in hydrogen-ion concentration which accompanied the initial decrease in conductance of these solutions may be taken as evidence that there was rapid absorption of hydrogen ion in the early part of each experimental period. As was the case with absorption in general, this was always greater the higher the concentration of the original solution, and greater the first day than in any succeeding day. Absorption of hydrogen ion by plant cells has been reported by many observers (**5, 14, 18, 19, 23**).

The toxicity of the hydrogen ion has long been recognized. About forty years ago KAHLENBERG and TRUE (**17**) pointed out that the toxic influence exerted upon plants by dilute solutions of strong acids was probably largely due to this ion. Since that time BREAZEALE and LECLERC (**3**), HOAGLAND (**16**), and DUNN (**12**), among others, have reported on acid toxicity for plant tissues. As to the effect of such toxicity within plant cells, ADDOMS (**1**) observed that the protoplasm of root hairs injured by an acid medium appeared to have been coagulated.

It seems probable that the toxic effects produced by the acid solutions of the present study were due chiefly to the hydrogen ion. Similar injuries appeared in all experimental plants and this was the only ion, other than the hydroxyl ion, which was common to all solutions. Also the hydrogen ion is more active, and probably more toxic, than any of the anions present.

In general, degree of toxicity followed hydrogen-ion concentration. For any acid the higher the concentration and the greater the ionic absorption therefrom, the more promptly did injury occur, and in the acids as a group it was generally true that the more completely dissociated the acid the more toxic it was. Propionic acid was, however, more toxic than would be expected from its ionic concentration or from the amount of ionic absorption that occurred from its solutions. Apparently the propionic molecule also was toxic. This is in agreement with TRUE'S (**25**) idea that the harmful action of formic and acetic acids is due principally to hydrogen ion, whereas that of propionic acid is due chiefly to the undissociated molecule. Other

workers also have attributed the toxicity of organic acid solutions to undissociated molecules (**6, 8, 12**). Even in the case of the acids whose toxicity seems to have been fundamentally due to excess of hydrogen ion, other ions or molecules may not have been without influence on toxicity.

The toxicity of these acids was generally greater at the higher temperature than at the lower. Injury was apparent earlier and the plants became more severely affected at the higher temperature. SKEEN (**21**) also has found toxicity to be increased by increase in temperature in some cases.

Although, as has been intimated, it appears likely that the initial decrease in conductance of the acid solutions was fundamentally due to hydrogen-ion absorption by the roots, there is indirect evidence that other ions and molecules also were absorbed. Furthermore there seems to be no reason to doubt that there was in all cases some exosmosis of ions or molecules, or both. That the initial lowering of solution conductance ceased—generally after 1 to 3 days for the mineral acids, and after a somewhat shorter time for the organic acids—must have been due to decreased absorption, to increased exosmosis, or to both together. Either of these alterations in the rate of movement of material across the root periphery may well have been occasioned by increasing toxic action. Indeed this increased exosmosis has been used as a criterion of injury by some workers (**8, 22**). With the mineral acids excessive exosmosis from the poisoned plants eventually became greatly pronounced, as was shown by increase in solution conductance, but no rapid outburst of electrolytes had occurred at the time the experiments with the organic acids were discontinued. Nor did rapid exosmosis occur within 8 days in solutions of aromatic acids tested in a similar way by MOTHER CHRYSOSTOM (**8**).

In those cases where conductance increased rapidly toward the end of the experimental period, the sudden increase in exosmosis that is indicated may have been due to a corresponding sudden increase in outward permeability of the root cells to electrolytes, such as might result from some sorts of poisoning, or perhaps poisoning may first have caused general protoplasmic coagulation, followed at length by a sudden disintegration. It is possible that the anions or undissociated molecules of the organic acids acted in some way to retard the poisoning process or hinder protoplasmic disintegration.

Summary

1. Roots of *Lupinus albus* were found to absorb electrolytes from very dilute solutions of certain inorganic acids—HCl, H_2SO_4, HNO_3—and certain organic acids—HCOOH, CH_3COOH, C_2H_5COOH. Absorption was greater in amount and more rapid the higher the original concentration of the solution. For any tested concentration it was greater as dissociation was more nearly complete.

2. There was apparently a rapid absorption of hydrogen ion, probably accompanied by some absorption of other ions, of molecules, or of both.

3. Injury to the plants resulted in all cases. This is probably to be attributed to absorbed hydrogen ion in each instance except that of propionic acid, whose undissociated molecules seem to have been largely responsible for the injury.

4. In many cases rapid exosmosis of materials from the roots eventually occurred, indicating increased permeability of cell membranes or rapid disintegration of cell contents.

5. Influence of temperature, solution concentration, and hydrogen-ion concentration on absorption and exosmosis and on growth and development of the seedlings are among the topics discussed.

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